AN ECOLOGICAL OVERVIEW AND CHECKLIST OF VASCULAR EPIPHYTES IN THE MONTEVERDE CLOUD FOREST RESERVE, COSTA RICA

Nalini M. Nadkarni

Department of Biological Sciences
University of California
Santa Barbara, California 93106 USA

Plants that dwell in the tree canopies of tropical cloud forests, and the fauna associated with them, have received a great deal of biological attention (e.g., Schimper 1903, Picado 1913, Huber 1974, Medina 1980, Benzing 1981, Dressler 1981, reviewed in *Brenesia,* Vol. 1).

Epiphytic plants, which derive support but not nutrients directly from their host trees, reach their greatest diversity and abundance in neotropical mid-montane forests and elfin woodlands (Madison 1977). The climatic conditions encountered there—high annual rainfall, a relatively short dry season, and the year-round frequent mist and fog-bearing winds—promote extremely rich epiphyte communities accompanied by thick mats of organic matter that they accumulate.

Nearly all accounts of cloud forest vegetation include descriptions of the epiphytic flora (Shreve 1919, Beard 1955, Richards 1964, Grubb and Whitmore 1965, Howard 1968, Leigh 1975, Whitmore 1975, Lawton and Dryer 1981). Cloud forest canopies are usually dominated by cryptogams, but over 10,000 species of vascular epiphytic plants are estimated to occur in these forests (Madison 1977).

Because of difficulties of access, epiphytes have been the focus of only a few studies of whole-ecosystem tropical forest ecology (Johansson 1968, Sugden and Robins 1979, Sanford 1968, Pócs 1980, Nadkarni 1981). Recent work in tree canopies of a variety of forest types, hower, have pointed out that their role in ecosystem-level interactions can be more important than previously considered due to their anatomical, morphological, and physiological characteristics (Lang *et al.* 1976, Benzing and Seeman 1978, Pike 1978, Nadkarni 1983).

Epiphytes have been shown to affect the forest ecosystem as a whole by their remarkable abilities to absorb and retain atmospheric nutrients borne in rain, mist, and dust. They are highly efficient at "straining" aerial mineral nutrients, incorporating them into their living tissues, and eventually transferring them to other parts of the ecosystem via herbivory, crownwash leaching, litterfall, and, in some cases, by host tree canopy root systems (Nadkarni 1981). This garnering of airborne moisture and nutrients is especially important during the dry season, when very little precipitation arrives as rain (Weaver 1972).

The presence of epiphytes may foster environmental conditions within the canopy that promote nitrogen-fixation. The increased humidity brought about by transpiring epiphytes may enhance conditions which promote the growth of free-living and symbiotic nitrogen-fixers; the water-retaining capacity of accumulated organic matter would also promote a suitable stratum for these organisms. Nitrogen fixed in the phyllosphere and on branch can be transferred by the pathways outlined above (Odum and Pigeon 1970, Forman 1975, Bentley in press).

In addition to their role in water and nutrient interception, epiphytes have been cited as a force in cloud forest dynamics, influencing forest structure and population changes. Heavy loads of epiphytes can increase the frequency of tree-and branch-falls; the resulting light gaps provide open areas for germination of new seedlings (Strong 1978). At present, there is little quantitative evidence to support or reject this hypothesis.

The epiphyte community also provides a source of food and habitat for a variety of birds, mammals, amphibians, reptiles, and insects, some of which depend exclusively upon epiphytic plant resources. A recent review by Gómez (19) documented over two hundred genera of animals utilizing epiphytic bromeliads.

Despite their potentially major impacts on various aspects of cloud forest ecology, epiphytes remain poorly known, ecologically and taxonomically. Of the estimated 15,500 neotropical epiphytic species (Madison 1977), many are as yet undescribed. As a preliminary step in augmenting the information available on epiphytes, I have compiled a checklist of plants collected by a number of biologists in the Monteverde Cloud Forest Reserve, a representative neotropical cloud forest of Costa Rica. This list is based on materials collected during a two-year study in the Reserve (Nadkarni in press). Also included are those plants residing at the Monteverde Herbarium whose labels identify them as being epiphytes. Other plants on the list were garnered from biologist familiar with Monteverde. Epiphytes were identified at various herbaria, and vouchers for most of them reside in the Monteverde Herbarium, presently located in the Visitor Center of the Reserve. Many of the local identifications were done by V. Dryer, R. Lawton, W. Haber, J. Beach, and L.D. Gómez.

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Resumen

Las epífitas –plantas que derivan apoyo físico pero no nutrientes de los árboles– pueden afectar el ecosistema del bosque nuboso entero por su habilidad de absorber y retener el agua y los nutrientes que pasan por la copa en forma de lluvia y niebla, por la carga pesada que puede precipitan caídas de árboles y ramas, y por la fuente importante de alimentación y un habitat para pájaros, anfibios, y otros animales que proveen. Sin embargo, las epífitas aún son poco conocidas. Se presente una lista de algunas que se encuentran en la copa del bosque nuboso de Monteverde, Costa Rica.

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Araceae
- *Anthurium davidsoneae* Standl.
- *Anthurium microspadix* Schott
- *Anthurium pittieri* Engl.
- *Monstera oreophila*
- *Philodendron* sp.
- *Stenospermation sessile* Engl.

Begoniaceae
- *Begonia estrellensis*
- *Begonia heydei* C.D.C.

Bromeliaceae
- *Achmaea* sp.
- *Guzmainia nicaraguensis*
- *Pitcainia* sp.
- *Tillandsia* sp.
- *Vriesia* sp.

Celastraceae
- *Euonymus costaricensis*

Ericaceae
- *Cavendishia capitulata* Donn. Sm.
- *Cavendishia complectans* Hemsl.
- *Cavendishia crassifolia* (Benth.) Hemsl.
- *Cavendishia endressii* Hemsl.
- *Cavendishia lactiviscida* Luteyn
- *Cavendishia quercina* A.C. Sm.
- *Disterigma humboldtii* (Kl.) Ndzu.
- *Gaultheria gracilis* Small
- *Gonocalyx pterocarpus* (Donn. Sm.) Standl.
- *Macleania ovata* Kl.
- *Psammisia ramiflora* Kl.
- *Satyria warszewiczii* Klotzsch
- *Themistoclesia smithiana*
- *Vaccinium poasanum* Donn. Sm.

Gesneriaceae
- *Besleria* sp.
- *Campanea humboldtii* (Kl.) Oerst.
- *Columnea glabra* (Oerst.) Hanst.
- *Columnea gloriosa* Sprague
- *Columnea lepidocaula* Hanst.
- *Columnea microcalyx*
- *Drymonia conocalyx* Hanst.

Guttiferae
Clusia alata Pl. & Tr.
Clusia palmana Standl.

Lentibulariaceae
Utricularia alpina Jacq.
Utricularia jamesonii

Liliaceae
Smilacina amoena Wandt.

Lobeliaceae
Burmeistera cyclostigmata Donn. Sm.
Burmeistera microphylla Donn. Sm.
Burmeistera tenuiflora Donn. Sm.

Loranthaceae
Gaiadendron punctatum (R. & P.) G. Don.
Phoradendron flavens (Sw.) Griseb.
Psittacanthus lateriflorus Woods. & Schery
Psittacanthus scheryi Woods.
Struthanthus oerstedii (Oliv.) Standl. & Cald.
Struthanthus quercicola (S. & C.) Blume

Marcgraviaceae
Marcgravia brownei (Tr. dpl.) Krug. & Urb.

Melastomataceae
Blakea anomala Donn. Sm.
Blakea gracilis Hemsl.
Clidemia striphnocalyx L.O. Wms.
Miconia sp.
Topobea sp.

Myrsinaceae
Grammadenia costaricana (Hemsl.) Mez.

Orchidaceae
Acostaea Pleurothalloides
Elleanthus aurantiacus (Lindl.) Reichb. f.
Elleanthus glaucophyllus Schltr.
Epidanthus paranthicus (Reichb. f.) L. Wms.
Epidendrum anoglossum Schlect.
Epidendrum difforme Jacq.

Orchidaceae
- *Epidendrum exasperatum* Reichb. f.
- *Epidendrum lankesteri* Ames
- *Epidendrum platystigma* Reichb. f.
- *Epidendrum polychlamys* Schltr.
- *Epidendrum subnutans* A. & S.
- *Erythrodes* sp.
- *Fregea amabilis* Schlecht.
- *Isochilus major* C. & S.
- *Lepanthus* sp.
- *Masdevallia ecaudata* Reichb. f.
- *Maxillaria umbratilis* L. Wms.
- *Pleurothallis cardiothallis* Reichb. f.
- *Pleurothallis ruscifolius* Jacq. R. Br.
- *Pleurothallis segoviensis* Reichb. f.
- *Pleurothallis tuerkneimii* Schltr.
- *Sobralia* sp.

Piperaceae
- *Peperomia angularis* C. DC.
- *Peperomia dotana* Trel.
- *Peperomia hylophila* C. DC.
- *Peperomia peltilimba* C. DC.
- *Peperomia pittieri* C. DC.
- *Peperomia pseudo-alpina* Trel.
- *Peperomia tenellaeformis* Trel.
- *Peperomia tetraphylla* (G. Forst.) Hook & Am.
- *Piper glabrescens* (Miq.) C. DC.

Rubiaceae
- *Hillia maxonii* Stand.
- *Psychotria parasitica* Sw.
- *Psychotria pithecobia* Standl.
- *Ravnia triflora* Oerst.

Saxifragaceae
- *Hydrangea asterolasia* Diels.
- *Hydrangea peruviana* Moric.

Solanaceae
- *Lycianthes synathera* (Sendt.) Bitt.

Ferns
- *Asplenium auriculatum* Sw.
- *Asplenium auritum* Sw.
- *Asplenium radicans* L.

Asplenium rutaceum (Willd.) Mett.
Blechnum fragile (Liebm.) Morton & Lell.
Cochlidium rostratum (Hook.) Maxon
Elaphoglossum spp.
Grammitis blepharodes (Max.) Seymour
Hymenophyllum elegantulum v.d. Bosch
Hymenophyllum microcarpum Desv.
Hymenophyllum polyanthanthos (Sw.) Sw.
Lomariopsis recurvata Fee
Nephrolepsis pectinata (Willd.) Schott
Peltapteris peltata (Sw.) Morton
Phlebodium aureum (L.) J. Sm.
Pleopeltis macrocarpa (Bory ex Wild.) Kaulf.
Pleopeltis percussa (Cav.) Hooker & Grev.
Polybotrya osmundacea H. B. ex Willd. in L.
Polypidium crassifolium L.
Polypodium (Grammitis) delitescens Schott
Polypodium duale Maxon [=*Grammitis serrulata* (Sw.)]
Polypodium fraxinifolium Jacq.
Polypodium hygiometricum
Polypodium (Goniophlegium) loriceum L.
Polypodium (Campyloneuron) repens Aubl.
Trichomanes radicans Sw.
Trichomanes polypodioides L.
Vittaria dimorpha K. Mull.
Vittaria graminifolia Kaulf.